JOURNAL
OF THE
BOMBAY NATURAL HISTORY SOCIETY

December 1997 Vol. 94 No. 3

BREEDING BIOLOGY OF THE GREAT PIED HORNBILL (*BUCEROS BICORNIS*) IN THE ANAIMALAI HILLS OF SOUTHERN INDIA[1]

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(*With one plate and two text-figures*)

Key words: hornbills, *Buceros bicornis*, Western Ghats, breeding, food, behaviour.

A great pied hornbill nest was observed for 183 hours in 1992 and 1993 in southern India. A total of 3,104 food items were delivered by the parent hornbills to the nest inmate(s), of which 2,265 (72.9%) were fig fruits. At least nineteen species of fruit and 7 species of vertebrate food were delivered to the nest. Fruit predominated in the food delivered throughout the nesting period, with more fruit in the initial than in the later stages. More animal food was delivered after the chick hatched than during incubation. Male nest visitation rate increased steadily through the weeks, reached a peak just after the chick hatched and then declined. Visitation rate was uniform through the morning hours, and no visits were made in the afternoon. Incubation period was 38 days. The entire nesting cycle lasted 102 days, shorter than in the northern population. It is hypothesized that females moult most of their feathers for thermoregulation and/or for space saving to increase variation in cavity choices.

INTRODUCTION

Although the great pied hornbill (*Buceros bicornis*) is fairly widespread in its distribution across south and southeastern Asia, little is known about its breeding biology in the wild. There have been some investigations in Thailand (Poonswad *et al* 1983, 1986, 1987; Tsuji *et al* 1987, Poonswad and Tsuji 1994), but none elsewhere, including peninsular India. The birds being large and conspicuous have inspired several useful anecdotal notes in the past (Tickell 1864, Hume 1890, Bingham 1897, Baker 1927, Ali 1936) but their excessively shy disposition, overall scarcity, and the largely inaccessible nature of the terrain they inhabit has probably impeded more detailed investigations. Captive breeding attempts around the world have provided additional information (Stott 1951, Poulsen 1970, Healy 1979, Choy 1978, 1980; Golding and Williams 1986) and some anecdotes of young hornbills as pets further contributed to our knowledge (Phipson 1898, Prater 1921, Ellison 1923). This paper describes observations made in 1993 on a single nest in southern India at the Anaimalai hills in the southern section of the Western Ghats (around 10°25'N lat.; 76°50'E long.). Supplementary information from other nests in the locality have also been included, with some data from the nest in 1992. This study focused on the duration and displacement of

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different phases of the unique nesting cycle, and the changes in the quantity and quality of food delivered to the nest inmate(s) by the parent(s) during these phases.

The population of great pied hornbills in southern India, which extends all along the Western Ghats from 18°N lat.,74°E long. (Ali and Ripley 1987), to the southern tip of the peninsula, is endangered, due to problems ranging from fragmentation of the wet forest habitat (Chattopadhyay 1985) to poaching of squabs and adults from nests (Alan Kemp and J.C. Daniel, pers. comm.; Ali and Ripley 1987). The species is included in Schedule I of India's Wildlife (Protection) Act, 1972 (CSE 1982).

Study Area

The study was conducted in Karian Shola, a patch of Southern Tropical Wet Evergreen Forest (Champion and Seth 1968) at an elevation of 750 m. For a description of vegetation, topography and wildlife of the area see, Vijayan (1979). The evergreen part of the forests comprise about 600 ha but the adjoining areas are covered by open forests, bamboo hill forests and teak plantations totalling 900 sq. km. The evergreen forest tract extends across two wildlife sanctuaries in different states: the Parambikulam Sanctuary in Kerala and the Indira Gandhi Sanctuary in Tamil Nadu. The nest, which was the subject of this study, was located about 100 m on the Kerala side of the inter-state border.

Methods

Observations were made from a camouflaged ground hide built about 20 m from the base of the nest tree. Field assistants helped in data collection. The nest was observed using 10X binoculars and occasionally an 8 to 32X zoom spotting scope. All activities of the birds were recorded using a micro-cassette recorder and later transcribed. Observations totalled 183 hrs. Most of the observations were made in 6 hr periods staggered throughout the breeding cycle. Except for three days in which the observations lasted into the afternoon, all observations were in the period between 0700 and 1300 hrs. Observations were not conducted past 1300 hrs because it was found that parental visitation virtually ceased in this period.

Seeds and other remains from the faecal debris beneath the nest (the midden) were regularly examined, collected, and identified as far as possible. Seeds were identified by the first author. Some of the seeds were identified by germinating them in a seedling nursery maintained in the camp. Those that were difficult to identify were sent to the Royal Botanic Gardens in England for identification and confirmation. Feather samples collected from nest middens at the base of nest trees were identified by an expert in the USA. Fresh weights of animal food delivered were obtained from Spector (1956). Statistical analyses were performed using SAS routines (SAS 1985) available on the IBM 4381 mainframe computer at the University of Arkansas: Analysis of Variance (ANOVA) with Duncan's Multiple Range, and Chi-square analysis.

Samples of hornbill cavity entrance plaster were collected for analysis to compare with soil and faecal matter. The analyses were conducted at the Department of Horticulture and Forestry, and the Agricultural Services Diagnostic Laboratory, University of Arkansas.

Observation and Discussion

Pre-nesting courtship

Great pied hornbills are a monogamous and territorial species (Kemp 1979). The first instance of courtship feeding of a female by a male was observed on 5th September, 1991. This was nearly five months before the female became sealed inside the study nest for the 1992 season. The courting pair was first seen with six other conspecifics on a fruiting *Ficus* tree. After one

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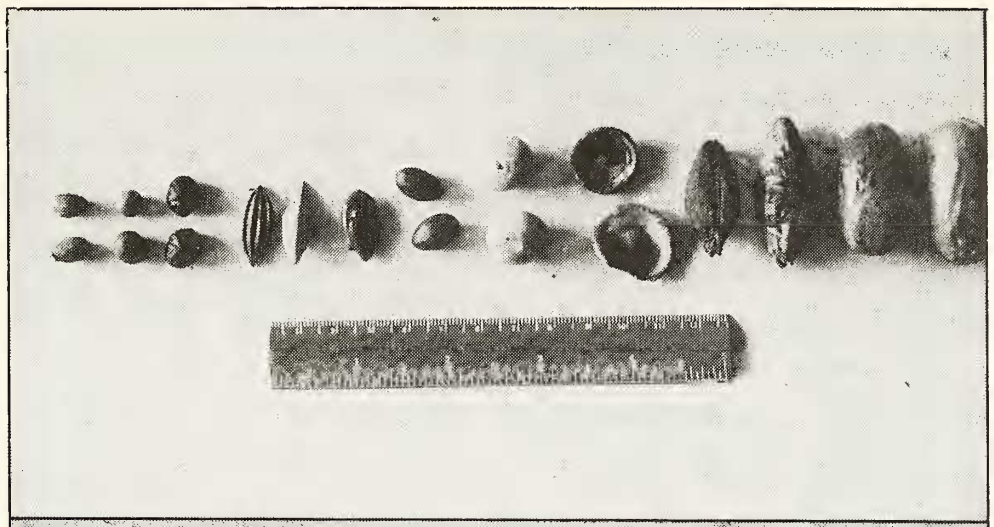

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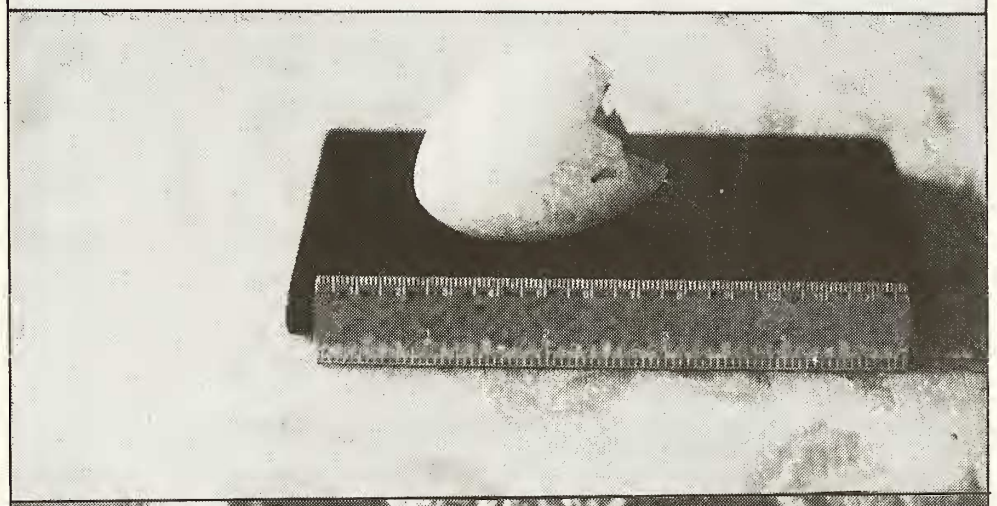

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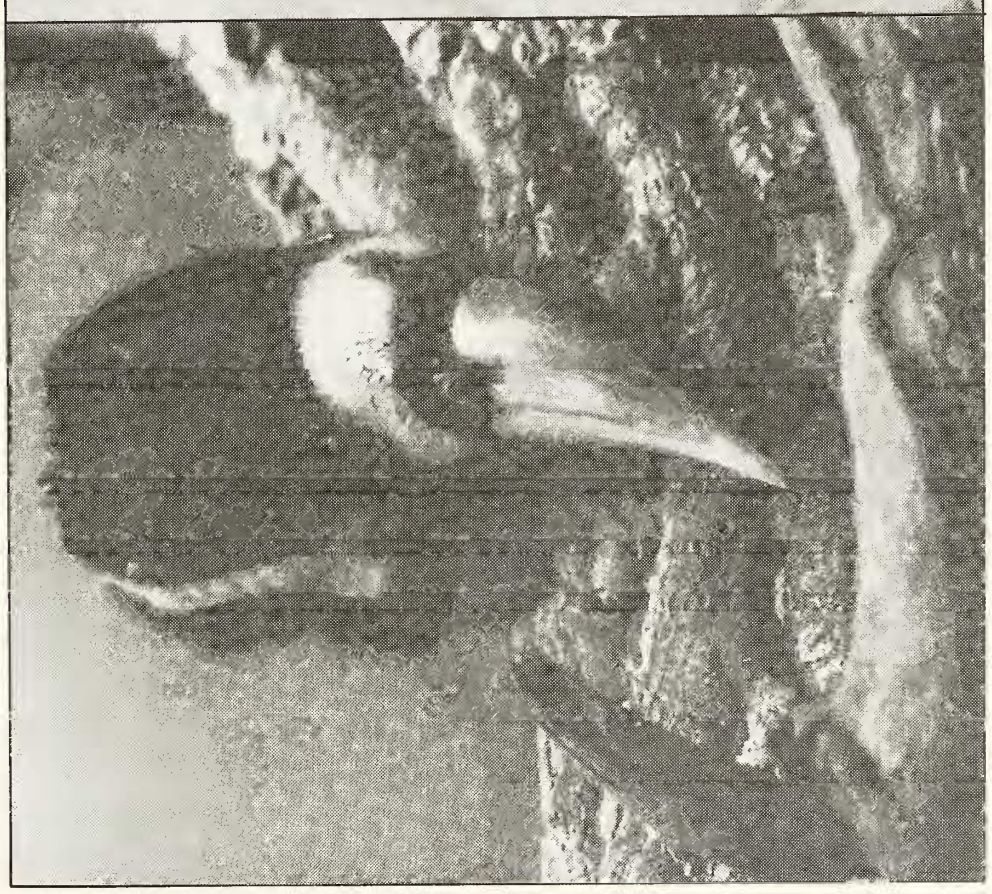

a. Seeds collected from the midden excreta at the base of the nest tree. b. Portion of egg discarded after hatching of chick, collected at the midden. c. Hornbill chick a few weeks after emergence from the nest cavity (courtesy of Bronx Zoo).

of the feeding bouts, the male flew to the top of a huge tree and was shortly joined by the female, which alighted on a branch about a metre below the male. The male then regurgitated something, presumably a fig, and offered it to the female perched below, which accepted it. Similar courtship feeding events were noted five times more that year. During one of the events, the male and female grappled with each other with bills locked, and emitted clapping sounds. Courtship feeding has been observed in Thailand (Poonswad *et al.* 1983, 1987) but the grappling behaviour was hitherto unknown. There is one very unusual record of mass "lek" like courtship behaviour in this species from southern India (Hutton 1986). No sign of male aggression towards rival males was observed.

The birds became exceptionally vocal after January. The breeding pairs indulged in vocal duets during the breeding season more than in the non-breeding season. The duets were performed mostly in the immediate vicinity of the nest. The following sequence of events characterized the duets: the male emitted a series of loud, resonant "kok" sounds, at a frequency of about one every other second, each "kok" uttered with head jerked back and bill pointing upwards. After three or four "koks", the female, which was invariably perched in a nearby branch, started a similar series of calls, with each "kok" emitted just prior to, or after, those of the male. This quickly became a mixture of hoarse roars and "barks" emitted by both birds in unison. Although the mixture of calls uttered in unison seemed haphazard, it was predictable, and remained unchanged through the season. Despite the commonness of these duets, they are not mentioned in the literature. This is possibly because they can easily be mistaken as the vocalizations of a single bird. Indeed, the synchrony in the calls and the difficulty in observing the birds through the lofty vegetation made it impossible to ascertain exactly the individual contribution of each bird in the duet.

The Nest, Clutch and Young

The nesting cavity was on a lofty *Alseodaphne semecarpifolia* (Lauraceae) tree in deep evergreen forest. Particulars of the nest site were: tree diameter, 72 cm; tree height, 35.15 m; nest cavity height, 17 m; cavity orientation, 242°; nearest human settlement, 1.5 km.

The cavity entrance was nearly circular in shape. Twenty three other nests located in the Anaimalai hills between 1991 and 1992 and information from 23 nests in Thailand (Poonswad *et al.* 1987) indicate a propensity of the birds to select a vertical slit entrance, with a width just wide enough for the casque of the female to enter. Just 4 out of 23 nests in Thailand and 6 out of 24 in the Anaimalai hills had circular entrances. At the present nest, there was a knob-like projection on the trunk on one side of the entrance, which provided a convenient perch for the male during nest visits. The male thus presented his profile while feeding the nest inmates, thereby greatly assisting the viewer in visual identification by the viewer of food material delivered. In the absence of such a perch site at other nests, the male was observed clinging on to the bark of the tree like a woodpecker, using the tail as a brace.

The nest and its contents could not be examined closely due to inaccessibility. Just one chick fledged in both the years of the study. Ali and Ripley (1987) reported that the clutch size in this species is "usually 2, sometimes 1", and Baker (1932) found that as many as 3 eggs could be laid on rare occasions. However, studies of other hornbills elsewhere have generally indicated that clutch size usually exceeds fledgling number, with the supernumerary eggs either not incubated, or their nestlings succumbing to sibling competition or parental neglect (Kemp 1971, 1976 as cited in Leighton 1986). Therefore, although no inferences can be made regarding the clutch size in the present study, it is possible that more than one egg was laid. Shortly after the chick hatched in 1993, the female discarded a large piece of egg shell, which we recovered from

the midden. The shell was dirty white and coarse textured.

Entrance Sealing

In both the 1991-92 and 92-93 seasons, the birds were first seen making short visits to the nest in early December, more than two months before the female bird became sealed in the cavity. Such early visits to the nest were seen at another nest in the same area. According to the local people, the parent birds clean the nest cavity by removing debris during these visits. This is supported by the appearance of old feathers beneath the nest cavity after inspection visits by the adult hornbills. The birds are exceptionally shy during such visits and may abandon a nest site if disturbed then. In December 1991, when the first author visited one of the nests, the parent birds became aware of his presence below the nest. Thereafter, the nest site was abandoned for that year (1992). However, the nest was reoccupied and was successful the subsequent year.

The actual sealing of the nest cavity entrance was not observed in either nesting season. By the second week of February, the female was ensconced inside the cavity. A small chunk of the wall broke loose and fell down sometime before 17th March, 1992, and this afforded an excellent opportunity to observe the female in the process of repairing the damage. The bird exclusively used its own excreta as a cementing material, with no mud deliveries from the male. Use of mud has been reported in the past for great pied hornbills (Stott 1951, Poulsen 1970, Ali and Ripley 1987). The bird turned around and deposited its excreta at the rim of the hole (instead of squirting it out as it usually does), and proceeded to apply portions of the excrement with its bill onto damaged area of the wall, using the flat side of the bill very much as a mason's trowel. The tapping sound produced by the bill as it plastered the sealing material was heard from below the tree. The female repaired the wall continuously until the wall was reconstructed. The wall had a mosaic of colours as the repairing was in progress. The dried intact sections were dark brown, and the wet "cement" was green and yellow. By the end of March the entire wall was complete, dry and uniformly brown.

Chemical analysis of the broken chunk of cavity entrance plaster that fell to the midden (Table 1) showed that the plaster closely matched the chemical composition of chicken and cattle faecal material (Spector 1956, Gerry 1968, Carey *et al.* 1993) and was very different from the nitrogen, total ash, and organic content of tropical soil (Sanchez 1976). This showed that the original plaster used to seal the cavity opening was also wholly faecal matter without an admixture of the soil reported in the past (see above). Thus, the original plaster was the same as what consti-

TABLE 1
COMPARISON OF HORNBILL PLASTER WITH FAECES AND TOP SOIL COMPONENTS (PERCENTAGES).

	Chemical element composition						Total ash	Total organic
	P	K	Ca	Mg	S	N		
Hornbill plaster	0.2	2.1	1.5	0.3	0.2	2.0	15.0	85.0
Chicken faeces	1.3	1.2	2.9	0.6	0.8	5.0	17.0	83.0
Cattle faeces	0.7	1.7	2.9	0.6	0.2	2.0	5.0	95.0
Tropical soil						0.2	96.0	4.0

tuted the repair work. (Chicken faecal matter was included in Table 1 to represent a bird, and cattle manure was added to characterize an animal with a vegetarian diet to compare with the fruity, mainly vegetarian diet of the hornbill.)

After the female left the cavity, the entrance was resealed exclusively by the young (which was 43 days old when the female left - see Figure 2). It was observed to use its excreta as the sealing compound, with no mud deliveries from the parents. The manner in which the young sealed the entrance was similar to that employed earlier by the female. It spent several hours of the day constantly tapping the wall.

Portions of the broken wall were collected from the midden below the nest and examined. The fragments had the consistency of cork and were uniformly embedded with hundreds of tiny fig seeds. Fig seeds occurred in all the 10 other nest-walls (from different nests) examined in the two seasons. The seeds apparently play an important role in holding the structure together, much like gravel in a concrete mix. (**Note**: This information about the great pied hornbill using excreta as sealing compound is what I (RK) reported to Kinnaird and O'Brien (1993), and not what they attribute to me concerning the Indian pied hornbill, *Anthracoceros albirostris*).

Feeding

At least 19 species of fruits and 7 species of vertebrates were delivered by the parent hornbills to the nest inmate(s) (see Appendix). A total of 3,104 food items were delivered by the male during the 155 hours of observation in the 1993 season. Of these, 2,265 (72.9%) were fig fruits, indicating the importance of the *Ficus* taxa during the breeding period. The study in Thailand also showed a predominance of figs in the breeding diet. Fifty-seven percent of the food items were figs in that case (Poonswad *et al.* 1987). Tables 2 and 3 show the pattern of food delivery during the three different phases of the nesting cycle, i.e., female only in cavity, female and young in cavity, and young only in cavity.

TABLE 2

DELIVERY OF FRUIT BY PARENT GREAT PIED HORNBILLS TO NEST OCCUPANT(S) DURING 1993

	Delivery rate per day*							
	Number of Items				Dry weight (gm)			
In Nest Cavity	Large figs	Small figs	Non figs	Total	Large figs	Small figs	Non figs	Total
Female only	0^{a}	$94^{a,b}$	88.6^{a}	182.6^{a}	0^{a}	12.22^{a}	NA	$12.22^{a,b}$
Female + Young (early)	14.5^{a}	205.7^{a}	53.5^{a}	273.7^{a}	20.1^{a}	26.7^{a}	NA	46.8^{a}
Female + Young (late)	22.2^{a}	8.2^{b}	6.6^{a}	37^{b}	30.8^{a}	1.06^{a}	NA	31.86^{a}
Young only	1.66^{a}	$37.5^{a,b}$	9.8^{a}	48.9^{b}	2.3^{a}	4.85^{a}	NA	7.15^{b}

*0700 to 1300 hrs

^{a,b}Reading vertically down the nesting phases, the means with the same letter(s) are not significantly different (Duncan's Multiple Range Test, á=0.05)

NA (not available)

For comparison, the female-young phase was further split as early and late for the analysis (Table 2). Figs were classified as "large" (>20mm diameter) and "small" (<20mm diameter).

The total number of fruit items delivered per day (Table 2) was significantly more in the female-only and the early part of the female-young phases than in the later phases of the cycle (ANOVA; $F_{3,16}$=6.78, P=0.003). Because figs predominated in the food, an analysis was done on the numbers and weights of figs delivered. The number of small figs delivered was significantly different between the early and late periods of the female-young phase, but no significant difference was found between the phases for the number of large figs or non-figs delivered (Table 2). Since fig numbers were confounded by different sizes and varying water content, fig dry weights were considered. Dry weights were obtained in the field for various species of figs by recording weights of sun-dried figs. No significant difference was found between the phases for the dry weights of large figs or small figs delivered per day. However, the total figs delivered in grams dry weight per day was significantly higher in the female-young (early and late) phase than the young-only phase (ANOVA; $F_{2,17}$=3.76, P=0.04) (Table 2).

Since fruit alone may not furnish the protein required for early fledgling growth, animal food is frequently used by frugivores to supplement the fruit diet of their nestlings (Skutch 1945, Welty 1982, Faaborg 1988). In this study, arthropods, reptiles, birds, and mammals were delivered to the nest occupant(s) (Table 3), arthropods throughout the nest cycle and the vertebrates more sporadically. An analysis of the total wet weights of animal food delivered per day (Table 3) showed that significantly greater amounts (χ^2_2=24.08, P<0.005) were delivered when the young and female were in the nest than when either the young or female were alone in the cavity. Such an increase in the delivery of animal food after the hatching of the chick has been reported in the past for hornbills of different species (Poonswad and Tsuji 1989).

TABLE 3
DELIVERY OF ANIMAL FOOD BY PARENT GREAT PIED HORNBILLS TO NEST OCCUPANT(S) DURING THE 1993 SEASON.

	Wet weight (gm/day*)				
In nest	Arthropods	Reptiles	Birds	Mammals	Total
Female only	.06	0	12	0	12.06
Female + young	.84	5.55	11	27.7	45.09
Young only	.21	16.64	0	0	16.85

*0700 to 1300 hrs

An overview of the food delivery data indicates that the hornbill nest occupants are given more fruits in the early part of the breeding period than in the later period, and animal food is delivered in increased quantities in the later part of the cycle. Results of phenological studies conducted concurrently in the study area showed a community peak in fruit production in the later part of the breeding cycle (April-May). This peak is brought about by the synchronous fruiting of several deep forest trees of the families Annonaceae, Myristicaceae, and Lauraceae. These fruits are relatively more nutritious than those produced by open forest trees (McKey 1975, Leighton and Leighton 1983) and were delivered by the parent hornbills to the young nestling at this time. It appears, therefore, that the reproductive cycle of the hornbill is synchronised with the community peak in fruit production. Thus, the phase when nutrition is needed the most, after the chick is hatched, coincides with peak fruit availability. The fact that animal food is delivered more at this time than in other phases, along with the overall preponderance of figs in the diet, suggests that a combination of high-quality fruits, figs, and animal matter is essential to meet the nutritional requirements of the growing chick. The nesting and

fledging of Great Pied Hornbills during the time of high fruit resource availability supported the findings of Leighton and Leighton (1983) and Leighton (1986) on Bornean hornbills. African *Tockus* hornbills, which feed mainly on arthropods, also breed during periods of high animal prey abundance (Kemp 1976).

Food was delivered by regurgitation except for the larger animal items, which were always carried in by the bill. The maximum number of fruits delivered in one load was 232, all small figs. Regurgitation resulted from pumping actions of the neck, and the fruits came out rapidly one by one, sometimes in twos and threes. Often, some of the fruits fell on the rim of the cavity, bounced off and accumulated in the midden at the base of the tree. These fruits were collected and examined, thus greatly facilitating confirmation of the material delivered by the male hornbill. After each visit, the male invariably flew to a nearby branch and wiped the bill by rubbing it against the boughs, before flying away for another consignment. Both female and young begged noisily, their quivering bill tips appearing at the cavity entrance, during the visits of the male. The begging was more vociferous each time the male appeared with large animal prey. The male was always seen to deliver the food directly to the female and not to the young (despite the young begging as actively as the female). It is presumed that the female in turn feeds the young, but how this happens could not be determined.

On 9th March, 1993, the male delivered 11 ripe *Strychnos nux-vomica* (Loganiaceae) fruits to the sealed-in female. The female later excreted the silvery discoid seeds which were collected from the midden. Bisset and Choudhury (1974) reported the occurrence of the CNS toxin strychnine in the pulp of ripe *Strychnos* fruits. Gamble (1922) reported that the toxin occurs in both pulp and seed, and that it is included in the diet of hornbills and monkeys. Janzen (1983) compiled evidence of such fruit traits and suggested that toxic fruits may be a regular component in the diet of some frugivores and seed-eaters (Munn 1994).

The male was seen and heard hunting for animal food in the vicinity of the nest more frequently after the chick hatched out than before hatching. It foraged in large trees, hopping from branch to branch, tearing down large flakes of dead bark in search of animal prey. Flakes of bark were held at the bill tip, examined for prey, and discarded; geckos or arthropods flushed from beneath the bark were caught, flicked up into the air, and gulped down. Larger prey were thrashed against the boughs to incapacitate them. Even in captivity, a breeding male actively pursued and captured a wild blackbird to feed its mate at nest (Golding and Williams 1986). In March 1992, when the open forests adjoining the study area were in flames, a male great pied hornbill was seen flying from a burning area towards the nest with a snake in its bill. The tendency of the male to investigate tree cavities regularly for animal prey is evident by the fact that this study yielded six incidences of the male hornbill delivering a Travancore flying squirrel (*Petinomys fuscocapillus*) to the nest. One of these records was based on the recovery of a partially eaten carcass from the midden. These squirrels are nocturnal, and spend the day sleeping in cavities. The great pied hornbill's habit of capturing animals from tree cavities has also been reported by Wood (1927) in which the hornbill devoured a brood of mynas from a hole, unperturbed by the attacks by the parents. In the present study, the male was seen delivering two altricial fledglings and one adult bird, and two other bird species were identified from the feathers collected at the midden (Appendix). The increased carnivorous habit of the hornbill in the nesting season makes it a feared predator in the forests. The male was frequently harassed by a pugnacious pair of racket-tailed drongos (*Dicrurus paradiseus*) in the vicinity of the nest. The hornbill seemed unperturbed by these attacks most of the time, but occasionally snapped at the

TABLE 4
DURATION OF MALE FEEDING VISITS TO NEST (MINUTES) OVER THE THREE DIFFERENT PHASES OF THE NESTING CYCLE.

In Nest cavity	Time spent at nest (Means ± SD)
Female only	4.43±1.93[a]
Female and young	3.7±2.21[a,b]
Young only	2.4±0.91[b]

[a,b] Means with the same letter are not significantly different (Duncan's Multiple Range Test, á=0.05);
SD = Standard deviation

drongos.

The mean duration of male visits to the nest was significantly different between the three main phases of the cycle (ANOVA, $F_{2,48}$=3.65, P=0.033) (Table 4). The male spent the greatest amount of time at the nest when the female was incubating, and the least amount of time when only the young was in the cavity. The mean time spent was significantly higher in the female-only phase than in the young-only phase (Table 4). No significant difference was found in the mean time spent in the female-young phase in comparison with either of the other two phases. This trend can be explained by the distinct difference in the time required for fruit and animal deliveries. The male spent an average of 4.12±2.12 minutes for each visit in which only fruit food was delivered (N=36), and 2.25±1.13 minutes for each visit in which only animal food was delivered (N=12). Since fruit predominated in the first half of the cycle, the male had to spend more time regurgitating the loads of fruit. Animal food deliveries, which increased in the latter half of the cycle, were usually done in a

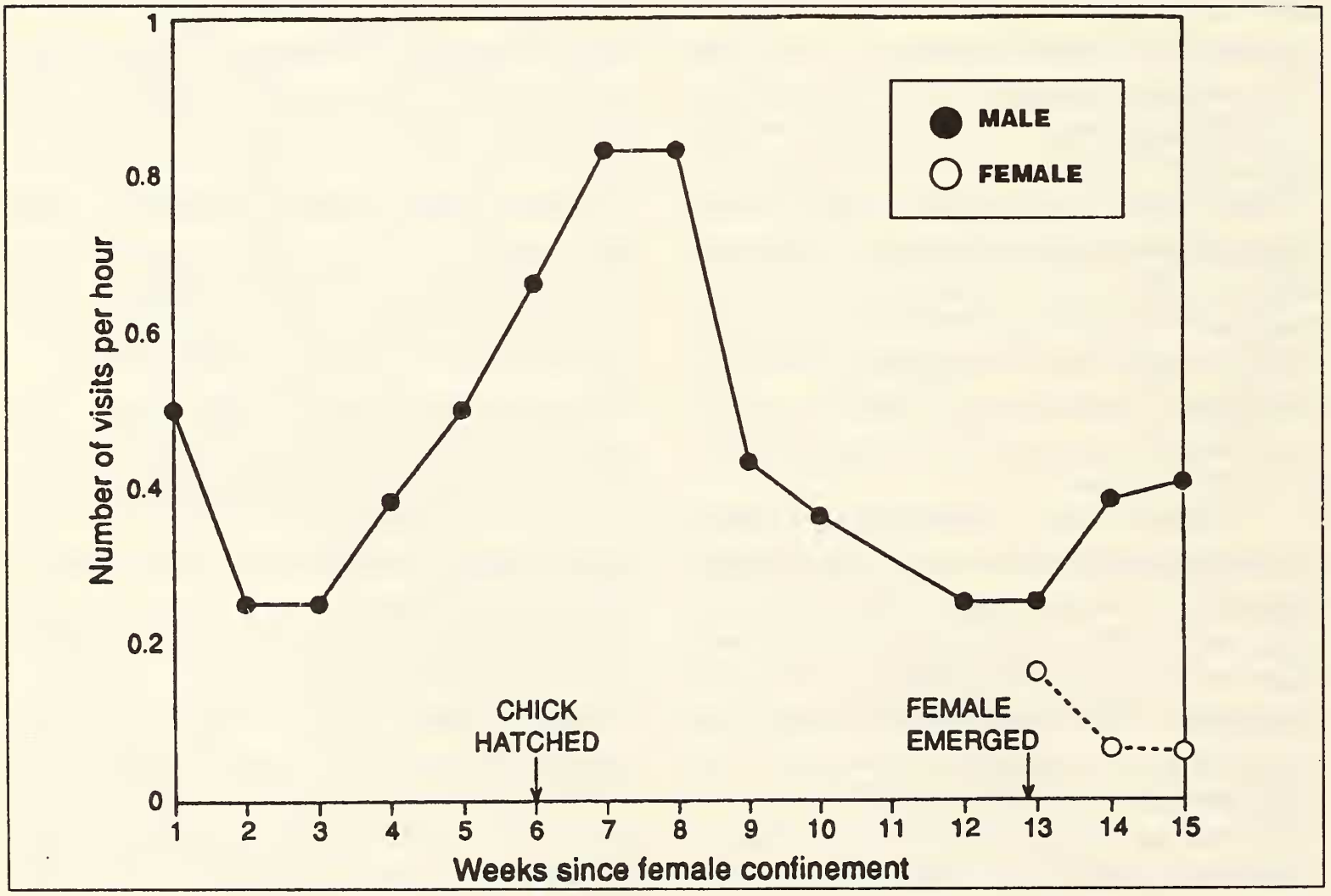

Fig. 1. Nest visitation rate by parent great pied hornbills during the 1993 season.

piece-meal manner and hence were of relatively short duration.

The male visitation rate to the nes increased steadily through time during the initial phase of the nesting cycle, reached a peak just after the hatching of the chick (6th week), and then progressively decreased as the chick developed (Fig. 1). This steady decline in feeding frequency may be a naturally evolved strategy of the parent to encourage the nearly fledged young to leave the nest (Welty 1982) before the onset of the monsoon (see later). The slight increase in male nest visitation rate as the chick neared fledging (Fig. 1) was because the male remained in the immediate vicinity of the nest in this period, and made frequent, short visits to the nest with relatively smaller amounts of food than earlier. From the 13th week onwards, after the emergence of the female, the provisioning responsibilities were shared by both the parents, but only to a very limited extent by the female. She seemed very weak after the three months of confinement. An increase in nest visitation rate after hatching was also reported by Poonswad and Tsuji (1989) for wild, and Choy (1980) for captive great pied hornbills. The former study also documented the general decrease in visitation rate (Fig. 1), as the chick aged.

Although no signs of non-human predation of hornbill nests was detected in the two years of investigation, the fact that the birds became exceptionally wary and circumspect at the advent of, and during, the breeding season indicates that human predation pressure may be a major influence on hornbill breeding behaviour. The decline in male visitation rate and duration of visits at nest after the hatching of the chick may at least be partly explained as precautionary responses against betrayal of nest to human predators.

Most of the nest provisioning was done in the morning hours. Male visitation virtually ceased in the afternoon. The male usually made one feeding visit to the nest late in the evening just prior to his roosting. The morning visitation frequencies out of a total of 57 visits were: 0700-0800 hrs, 21.0%; 0800-0900 hrs, 15.7%; 0900-1000 hrs, 22.8%; 1000-1100 hrs, 14.0%; 1100-1200 hrs, 17.5%; 1200-1300 hrs, 8.7%. This pattern of visitation supported the hypothesis of equal visitation rates through the morning hours (χ^2_5=4.368, P>0.05). Due to the distance from the nest, observations of the nest could not begin earlier than 0700hrs. It is possible that at least one visit occurred shortly after day break each day. Fresh excreta was often found at the midden at 0700hrs.

Nest sanitation

The confined female, and later on the chick too, ejected excreta with force through a slit in the partially sealed cavity opening. The excrement accumulated in a wide area near the base of the tree. These middens and the undigested seeds therein, were an important source of information on the identity of food delivered to the nest inmates. Ant swarms and rodent pellets were often seen in the middens, suggesting regular seed removal by these agents. The midden emitted a distinct fruity odour. The young bird was not observed to expel the excreta until it was 2 weeks old. Since the female spent a considerable amount of time cleaning the nest by throwing out debris, it is presumed that the female threw out the faecal matter of the young during this time.

Fledging

The chick left the nest cavity on 28th May after 65 days of confinement (Fig. 2). The actual emergence of the chick from the nest was not observed, but a local tribesman reported that he saw one of the parent birds tear down the wall of the nest to help the chick come out. The chick remained in the vicinity of the nest, perched sedately in a nearby tree and provisioned by both parents, for several hours after emergence from the nest. It was seen preening continuously and occasionally snapping at the air (after insects?).

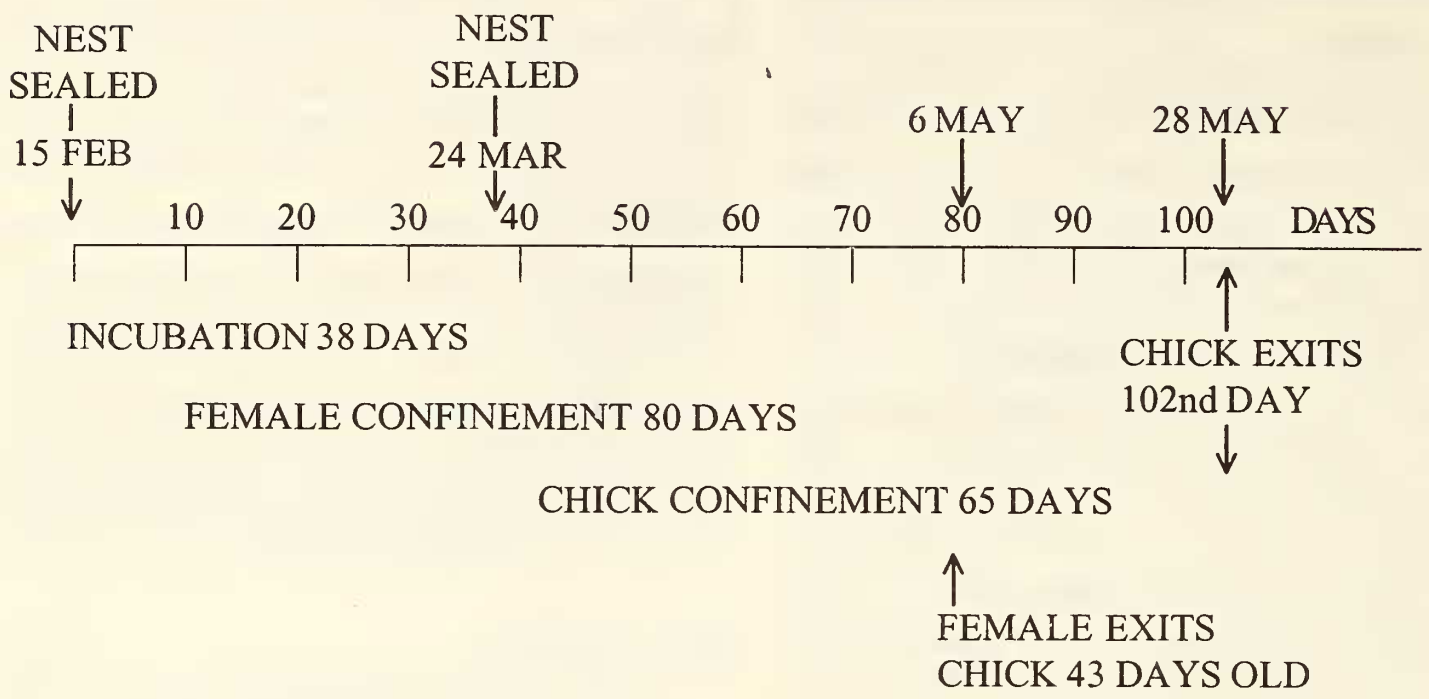

Fig. 2. Nesting schedule of the great pied hornbill during the 1993 season.

It begged actively when the parents were nearby. The bill was yellowish, with the upper mandible tinged with red, and had no casque. The eyes were yellow. The bird appeared tidy and well groomed, but occasionally moved clumsily between branches. The parents roared agitatedly at the slightest sign of human intrusion in the area. Neither the parents nor the young were seen the next day in the area, and it was not possible to visit the area from then on. A radio-tracked chick in Thailand remained within 2 km of the nest for several months after fledging (Tsuji *et al.* 1987). Studies of the similar, forest dwelling *Buceros rhinoceros* in Borneo (Leighton 1986) indicate that the young may stay with and be fed by the parents for upto six months after fledging.

Moult

The rectrices of the female, which could be seen through the cavity entrance just before the ejection of excreta, remained intact throughout the breeding cycle. However, the 4 or 5 large flight feathers (some of them soiled and unkempt) removed from beneath the nest indicate at least a partial moult. Tickell (1864) and Ali and Ripley (1987) reported a complete simultaneous moult of all flight feathers (rectrices and remiges) by the confined female, whereas Poonswad *et al.* (1983) recorded females with both a complete moult and no moult at all of flight feathers. It appears, therefore, that the extent of this moult is variable.

There are possible explanations for the complete or near-complete moult of breeding female great pied hornbills. Since the breeding occurs in the hot season and because the female is sealed in the nest cavity, such a moult may help the bird to maintain optimal body temperature without the risk of overheating. The maximum temperature recorded in the study area during the months of February, March and April 1993, the period the female was sealed in, was 32.2, 32.2, and 34.4° C respectively. Another possible explanation can be the scarcity of large nest cavities, which imposes a constraint on the breeding of these birds. This problem may be solved by the moulting of all or most of the feathers by the confined female resulting in body size reduction. Such a size reduction may increase the variety of choices from available cavities. This hypothesis is consistent with the

TABLE 5
DURATION OF THE DIFFERENT PERIODS (NUMBER OF DAYS) OF THE BREEDING CYCLE: A COMPARISON WITH PREVIOUS STUDIES.

Nest status	Present Study 1992	Present Study 1993	Previous studies	Captive (C) or Wild (W)	Place & Source
Incubation	38	38	40	W	Thailand, Poonswad *et al* (1987)
			38	C	U.K.,Golding & Williams (1986)
			40	C	Singapore, Choy (1980)
Female in nest cavity	53	80	114-134	W	Thailand, Poonswad *et al* (1987)
			112	C	Singapore, Choy (1980)
			77	C	U.K.,Golding & Williams (1986)
Age of young when female exits cavity	16	43	35+	C	U.K., Golding & Williams (1986)
			37-69	W	Thailand, Poonswad *et al* (1987) India, Ali and Ripley (1987)
Young in nest cavity	NA	65	70+	C	U.K., Golding & Williams (1986)
			72-96	W	Thailand, Poonswad *et al* (1987)
			96	C	Singapore, Choy (1980)
Entire nest cycle	NA	102	±140	W	Thailand, Poonswad *et al* (1987)
			110	C	U.K., Golding & Williams (1986)
			138	C	Singapore, Choy (1980)

NA (not available)

fact that adult female great pied hornbills are slightly smaller than males (Ali and Ripley 1987). (Because only a few of the moulted flight feathers were found beneath the nests, it is assumed that the female uses the other moulted feathers to line the nest cavity.)

Nesting Schedule

The entire nesting cycle in 1993 took 102 days from female confinement to chick emer-

gence from the nest (Table 5, Fig. 2). Assuming that the egg is laid shortly after female confinement, the incubation period was estimated to be 38 days in both the years the nest was studied (Table 5). The date of hatching was assumed to be the day the presence of the chick was first detected by hearing begging calls or seeing its bill at the cavity entrance. The length of incubation agreed closely with that found in previous studies, but the female confinement period was strikingly short for the present nest in both years compared with most of the previous studies (Table 5). This seems to indicate that female great pied hornbills in southern India may stay in the nest cavity for a shorter time than their northern conspecifics. Could it be that an incomplete moult enabled the birds to stay in for a shorter time? Possibly, the pressure of the comparatively frequent predation by indigenous people in the southern Indian range than elsewhere has shortened the female's stay in the nest, thus reducing its period of vulnerability (V. Santharam, pers. comm.). Early emergence of the female could also indirectly benefit the young by enhancing its provisioning and thus hastening its own emergence from the nest cavity. In 1992, the female left the nest when the young was just 16 days old, corroborating the findings of Ali and Ripley (1987) (Table 5). The duration of the young's stay in the nest was also shorter in this study than in all the previous studies. A comparison with studies on the wild population in Thailand (Table 5) indicates that the length of the entire cycle might be shorter in the southern than in the northern populations. In this study, in the southern range of the hornbill, the length of the nesting cycle certainly was shorter than in other studies (Table 5, Fig. 2).

Monsoon patterns could also explain the reason for the apparently short nest cycle in the southern population. Birds that nest in tree cavities, as well as ground nesting species, must complete their parental duties before the onset of the southwest monsoon (Ali 1979). This monsoon brings most of the rains to the Indian subcontinent, beginning in early June in southwestern India, and sweeping across the subcontinent in a northeasterly direction. Heavy rainfall thus occurs several weeks earlier in southern India than elsewhere, making it important for birds to finish nesting before the end of May, thus evading the disruption caused by extensive heavy rains and high winds.

Implications for conservation

The extended breeding cycle and slow rate of recruitment of great pied hornbills makes them an example of K-selected species and thereby renders them vulnerable to extirpation. The undoubted requirement of mature, deep forest trees with natural cavities large enough for occupation by the female and the chick imposes severe constraints on breeding opportunities, especially in the wake of the heavy deforestation and selective removal of large trees for timber in the peninsular Indian range. Poaching by locals of the helpless female, and more often the squab, from the nest, which was found to be regular in some areas of the range (Kannan 1993, 1994), could seriously affect densities and recruitment rates in those areas. Removal of fig trees to feed captive elephants engaged in lumbering operations, which occurs regularly all over the range, could limit foraging opportunities for hornbills. Given the preponderance of figs in the breeding diet, along with the keystone characteristics of the fig taxa (Kannan 1994), the importance of conserving fig trees cannot be overemphasized in any conservation scheme to maintain hornbill populations

ACKNOWLEDGEMENTS

J. C. Daniel of the BNHS first suggested the topic and was of invaluable assistance throughout the duration of the project. Financial support for field work in India was provided by the New York Zoological Society and Ornitholidays (through the Oriental Bird Club, U.K.). Travel grants came from

Dr. R. Balachander, the Arkansas Audubon Society Trust, and the University of Arkansas. Field work in India was greatly helped by assistance from Divya Mudappa. Dr. Roxy Laybourne of the U.S. Fish and Wildlife Service identified feather samples. Dr. Gren Lucas of the Royal Botanic Gardens, U.K. helped in seed identifications. Dr. V.S. Ramachandran of the Kongunadu Arts and Science College, Coimbatore, helped with plant taxonomy. Special thanks to the Tamil Nadu Forest Department officials for permission to work in the sanctuaries of the state and for their active cooperation. Dr. G. L. Wheeler, and the Agricultural Services Diagnostic Laboratory, University of Arkansas, performed chemical analyses on the hornbill cavity entrance plaster, and Dr. Paul R. Nolan gave information on faecal composition of poultry and cattle. The statistics benefited from comments from Miguel Armella. Dr. Alan Kemp and V. Santharam made useful comments on an earlier version of this manuscript. Special thanks to T.R. Sridhar for his reviews of several drafts of the paper. Dr. Alan Kemp and Dr. Pilai Poonswad for literature; Shekar Dattatri introduced us to some very helpful tribal people. The Kadar tribals of the Anaimalai hills played a major role in the project by discovering nests.

APPENDIX

List of fruit and vertebrate taxa delivered by parent great pied hornbills at the nests in 1992 and 1993.

I. FRUITS:

Family Moraceae:

1. *Ficus mysorensis*
2. *Ficus tsiela*
3. *Ficus* sp.

Family Lauraceae:

4. *Persea macarantha.*
5. *Alseodaphne semecarpifolia*
6. *Litsea oleoides*
7. *Cinnamomum* sp.
8. *Beilshmedia wightii*
9. *Beilshmedia bourdilloni*

Family Ebenaceae:

10. *Diospyros montana*

Family Loganiaceae:

11. *Strychnos nux-vomica*

Family Myristicaceae:

12. *Myristica* sp.

Family Annonaceae:

13. *Polyalthia* sp.

Family Bixaceae:

14. *Scolopia crenata*

Family Sapotaceae:

15. *Chrysophyllum* sp.

Family Sapindaceae:

16. *Filicium decipiens*

Family Burseraceae:

17. *Canarium strictum*

Family Elaegnaceae:

18. *Elaegnus conferta*

Family Oleaceae:

19. *Olea dioca*

II. VERTEBRATES:

Reptiles	:	1. Snake
		2. Lizard (Agamid)
		3. Lizard (Gecko)
Birds	:	1. Barred Jungle Owlet *Glaucidium radiatum*
		2. Grey-fronted green pigeon *Treron pompadora**
		3. Collared scops owl *Otus bakkamoena**
		4. Unidentified yellow feather
		5. Unidentified altricial fledglings
Mammals	:	1. Flying Squirrel *Petinomys* sp.

* feathers recovered from midden